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Response of carbon fluxes to water relations in a savanna ecosystem in South Africa

W. L. Kutsch¹, N. Hanan², R. J. Scholes³, I. McHugh⁴, W. Kubheka²,
H. Eckhardt⁵, and C. Williams²

¹Max-Planck-Institute for Biogeochemistry, P.O. Box 10 01 64, 07701 Jena, Germany

²Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, USA

³Council for Scientific and Industrial Research (CSIR) Natural Resources and the Environment PO Box 395 0001 Pretoria South Africa

⁴School of geography and environmental science, Monash University, Clayton, Australia

⁵South African National Parks (SANParks), Scientific Services, Skukuza, South Africa

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Correspondence to: W. L. Kutsch (wkutsch@bgc-jena.mpg.de)

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Abstract

The principal mechanisms that connect carbon fluxes with water relations in savanna ecosystems were studied by using eddy covariance in a savanna ecosystem at Kruger National Park, South Africa. Since the annual drought and rewetting cycle is a major factor influencing the function of savanna ecosystems, this work focused on the close inter-connection between water relations and carbon fluxes. Data from a nine-month measuring campaign lasting from the early wet season to the late dry season were used.

Total ecosystem respiration showed highest values at the onset of the growing season, a slightly lower plateau during the main part of the growing season and a continuous decrease during the transition towards the dry season.

The regulation of canopy conductance was changed in two ways: changes due to phenology during the course of the growing season and short-term acclimation to soil water conditions.

The most constant parameter was water use efficiency that was influenced by VPD during the day but the VPD response curve of water usage did change only slightly during the course of the growing season and decreased by about 30% during the transition from wet to dry season.

The regulation of canopy conductance and photosynthetic capacity were closely related. This observation meets recent leaf-level findings that stomatal closure triggers down-regulation of Rubisco during drought. Our results may show the effects of these processes on the ecosystem scale.

1 Introduction

Savannas are defined as tropical and sub-tropical vegetation types where woody plants and grasses co-dominate. They are characterized by a seasonal change of water availability with distinct rainy and dry seasons. Decades of research have identified not

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only water, but also nutrients, herbivory, and fire as major drivers of savanna vegetation dynamics (Walter, 1939, 1971; Scholes and Walker, 1993; Scholes and Archer, 1997; Sankaran et al., 2004; Sankaran et al., 2005; Beerling and Osborne, 2006).

Despite large land surface coverage (~20% of the global land surface and 40% of the African surface), important biodiversity (~8000 of 13 000 African plant species are savanna endemic, White 1980) and substantial land use change in savannas, there have been relatively few projects focussing on the patterns and processes controlling savanna carbon and water vapour exchange (Levy, 1995; Verhoef et al., 1996; Lloyd et al., 1997; Hanan et al., 1998; Scanlon and Albertson, 2004; Veenendaal et al., 2004; Williams and Albertson, 2004; Williams and Albertson, 2005 for African savannas; Meir et al., 1996; Miranda et al., 1997; Meinzer et al., 1999; da Rocha et al., 2002; Santos et al., 2003 for South American savannas; (Hutley et al., 2000, 2001, 2005; Chen et al., 2002, 2003; Beringer et al., 2003 for Australian savannas; and Baldocchi et al., 2004 for temperate Mediterranean savannas in California).

Increasing our understanding of the physical and physiological controls on savanna functioning using eddy covariance measurements is of great importance both for fundamental ecological understanding as well as for improved management and conservation of these important ecosystems. Such measurements will, furthermore provide basic data for refining models of ecosystem carbon dynamics and facilitate improved understanding of the role of tropical savannas in global carbon cycles, as well as informing policies related to the role of African countries in Kyoto Protocol.

One of the few infrastructures enabling the study carbon and water relations of African savannas is the flux tower in the Kruger National Park, installed between Skukuza and Pretoriuskop in 2000 as part of the Safari 2000 campaign (Otter et al., 2002; Shugart et al., 2004). The site is located at the boundary of two plant communities, representative of the main division within African savannas between broad-leaved eutrophic and fine-leaved dystrophic savannas (Scholes, 1990). When the wind blows from the SE (105°–196°), a fine-leaf *Acacia* savanna is sampled, and when it blows from the N (270°–76°), a broad-leaf *Combretum* savanna is sampled. These two wind

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directions are approximately balanced, and contribute over 80% of wind movement at the site. Sectoral analyses of eddy covariance measurements have been conducted successfully in previous studies (e.g. Kutsch et al., 2005).

In this study we investigate principal mechanisms that connect carbon fluxes with water relations in savanna ecosystems and differences between the two savanna types. Since the annual drought and rewetting cycle is a major factor influencing the function of savanna ecosystems, this work is focused on two questions concerning water relations:

1. How do water availability and seasonality drive ecosystem respiration?; and
2. how does the close inter-connection between canopy conductance and photosynthesis, influence the carbon uptake by the vegetation during times of different water availability?

Ecosystems respiration as measured by the eddy covariance technique is the sum of soil, plant, and animal respiration. Soil and plant respiration are typically found to respond to air or soil temperatures (Arrhenius, 1915). Soil temperature at 2 cm depth has been identified as the environmental factor best correlating with ecosystem respiration in many studies (Aubinet et al., 2000; Kutsch et al., 2005; Reichstein et al., 2005). In most cases it explains a high proportion of (short-term) temporal variation in ecosystem respiration at a given site. The influence of temperature on respiration is often described as an exponential relationship, characterised by the Q_{10} parameter (van 't Hoff, 1898). In many studies, this exponential equation provides a good fit to the temperature-respiration relationship at short timescales.

In biomes with a pronounced rainfall seasonality and/or water limitation, the temperature response may be secondary to the response to water availability. Additional factors influencing respiration may also co-vary with temperature, making it difficult to attribute effects. For example, during the rainy season in semi-arid systems increased biomass and physiological activity in plants and rhizosphere results in increased respiratory fluxes. In cases where temperature co-varies with rainfall, plotting the temperature re-

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sponse curve of respiration for an entire year may indicate a high apparent Q_{10} value which may be caused more by biomass and productivity changes than by temperature. A thorough analysis of seasonal patterns of ecosystem respiration is necessary to reveal these subtle interactions.

5 Ecosystem photosynthesis is likewise controlled by a complex interaction of processes that connect carbon fluxes and water relations. The control of CO_2 and water vapour exchange between ecosystems and the atmosphere by the stomatal aperture of plant leaves is the hinge between the two cycles – particularly notable in arid and semi-arid biomes. Stomatal conductance is regulated by a complex system of feedback and
10 feed-forward mechanisms (Jarvis, 1976; Cowan and Farquhar, 1977; Raschke, 1979; Ball et al., 1981; Lösch and Tenhunen, 1981; Ball et al., 1987; Leuning, 1995) involving environmental and internal factors. Several hypotheses exist regarding the 'goal' of stomatal regulation (Jones, 1998). It may function to (i) minimise water loss associated with CO_2 uptake (Cowan and Farquhar, 1977), (ii) avoid xylem cavitation or other
15 damaging results of plant water deficits (Tyree and Sperry, 1988), and/or (iii) allow transpiratory cooling of leaves to minimize heat stress (Burke et al., 1988). Stomatal conductance of a leaf depends on irradiance, temperature, air humidity and internal concentration of CO_2 . However, the same stomata do not always react to the short-term (diurnal) variations of these environmental factors in the same way. Leaf stomatal
20 sensitivity can be modified within periods of several days or weeks by phenology and by acclimation to factors such as soil water status (Halldin et al., 1984). Several recent publications have suggested that stomata acclimate directly to microclimate variations across days to weeks. For example, Kutsch et al. (2001a) assessed the influence of mid-term stomatal acclimation on ecosystem fluxes by calculating canopy water and
25 carbon balances for several years under different climates. Frechilla et al. (2004) provided evidence with molecular tools that guard cells acclimate at the same time scale. If acclimation is universal for stomata regulation of higher plants, it should be prominent in savanna ecosystems and should appear as a strong control of carbon and water exchanges (Williams and Albertson, 2005). This study uses the approach developed by

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Kutsch et al. (2001a) to evaluate stomatal acclimation at the canopy level.

By combining the regulation of respiration on one hand and stomatal conductance and photosynthesis on the other we provide a principle analysis of the regulation of savanna carbon fluxes by water relations. We used data from a nine months period measured in the year 2003 for this study. The eddy-covariance system was started at 8 January 2003 and running throughout the year 2003 until the tower was struck by a lightning in early September. All instruments were affected and had to be sent overseas to be fixed.

2 Methods

2.1 Research site

The Skukuza flux tower was established in early 2000 to study the carbon, water and energy dynamics of semi-arid African savannas and, in particular, how biogeochemical pathways differ in the nutrient rich fine-leaf savannas and nutrient poor broad-leaf savannas that are typical of much of Africa (Scholes and Archer, 1997). The site was also part of the SAFARI 2000 experiment to understand the interactions between the atmosphere and the land surface in southern Africa by connecting ground data of carbon, water, and energy fluxes with remote sensing data generated by Earth Observing satellites (Otter et al., 2002; Scholes et al., 2001; Shugart et al., 2004). The location of the tower is about 13 km W of Skukuza in the N'waswitshaka catchment, an ephemeral tributary of the Sabie River. The altitude of the site is 365 m above sea level. The underlying parent material is Archaean granite and gneiss. The landscape shows a typical undulating form with drainage lines about 3 km apart and ridge tops about 40 m above valley floors. This leads to a catenal pattern of soils and vegetation, with nutrient-poor *Combretum* savannas on the crests, and nutrient-enriched *Acacia* savannas on the lower parts of the slope.

Detailed soil and vegetation analyses of the two types are given in Scholes et

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al. (2001). They show that the soil in the *Acacia* savanna contains more clay, more nutrients such as nitrogen and phosphorous and also a higher cation exchange capacity than in the *Combretum* savanna. Volumetric field capacity (WC_{FC}) is about 0.12 in the *Combretum* – and 0.2 in the *Acacia*-savanna. Volumetric water content at –1500 kPa (“wilting point”, WC_{WP}) was 0.06 and 0.1, respectively. Relative plant available water (RPAW) was calculated from the actual volumetric water content for the layers 0–10 cm and 0–30 cm by

$$RPAW = \frac{(WC_{akt} - WC_{WP})}{(WC_{FC} - WC_{WP})} \cdot 100 \quad (1)$$

Rainfall at the site averages 547.1 mm but with significant interannual variability. The first precipitation events of the rainy season generally occur in late September or October, with last rains in April or early May. However, much of the interannual variability in total precipitation arises with variation in the dates of first and last rains. Figure 1 shows the long-term monthly means of minimum and maximum temperature and the mean precipitation at Skukuza (data from 1960–1999, after Scholes et al., 2001). Precipitation is shown as cumulative curve. In order to show a complete growing season the data are printed from August to July. Most of the annual rainfall occurs during the summer (October to April). In the lower part of Fig. 1 the monthly precipitation of the growing season 2002/2003 is compared to the long-term mean. The 2002/2003 growing season was very dry. Only half of the long-term amount of rain fell (276 mm).

The vegetation of the study site is open woodland with approximately 30% tree canopy cover in both *Acacia* and *Combretum* savanna types (Scholes et al., 2001). Leaf area index of the trees in both savanna types is similar, increasing to an area average of approximately 1.0 (i.e. within canopy LAI~3.0) three or four weeks after the beginning of the rainy season and then remaining at that level until several weeks after the last rainfall. Thereafter, the trees in the *Combretum* savanna drop their leaves, whereas the *Acacia* species remain leafy during the dry season. Herbaceous layer productivity and LAI is more dynamic with inter-annual variability in total rainfall, with

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average LAI of the herbaceous layer similar to the tree layer (i.e. 1.0), but in this case spread out more or less evenly across the landscape rather than being confined within the tree canopies.

2.2 Eddy covariance system

5 Ecosystem-level fluxes of water, heat and carbon dioxide were made using a closed-path eddy covariance system mounted at 16 m. This consisted of a 3-dimensional sonic anemometer (Gill Wind Master Pro, Gill Instruments, Lymington, UK) to measure fluctuations in horizontal and vertical wind speeds (m s^{-1}) and temperature (K), and a gas analyzer (LiCor 6262, LiCor, Lincoln, Nebraska, USA) to measure carbon dioxide
10 ($\mu\text{mol mol}^{-1}$) and water vapour (mmol mol^{-1}) concentrations. The gas samples were drawn at 6 l min^{-1} through a 6 m teflon-coated tube to the gas analyzer enclosed in a weather-proof box. The sonic anemometer and gas analyser measurements were recorded at 10 Hz, but we used the dilution and pressure-broadening corrections of the gas analyzer to compute concentrations that slowed the temporal resolution of the
15 scalar measurements to 3–5 Hz.

2.3 Supplemental measurements

Additional weather measurements on the main tower included measurements of incident and reflected shortwave radiation ($300\text{--}1100 \text{ nm}$, W m^{-2} , CM14, Kipp and Zonen, Delft, The Netherlands), incident and reflected near-infrared ($\text{CM14 } 600\text{--}1100 \text{ nm}$, W m^{-2} , Kipp and Zonen, Delft, The Netherlands) and incoming and emitted longwave radiation ($\text{CG2, } >3.0 \text{ nm}$, W m^{-2} , Kipp and Zonen, Delft, The Netherlands). Radiation measurements were made at 20 s intervals and then recorded in the data-logger as
20 30 min averages. By difference between solar and near-infrared radiation (NIR) measurements we estimate incident and reflected photosynthetically active radiation (PAR, W m^{-2}). Precipitation events were recorded with a tipping-bucket raingauge (Texas Instruments TE525, mm) totalled for each 30 min period.
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In addition to the meteorological and flux measurements on the main tower, we deployed two smaller towers to measure volumetric soil moisture and temperature in the adjacent *Acacia* and *Combretum* savannas. In each savanna we deployed TDR probes (Campbell Scientific CS615, cm³ water cm⁻³ soil) and temperature probes (Campbell Scientific 108, °C) in profiles with 4 or 5 measurement depths from near the soil surface to just above bedrock.

2.4 Data treatment

Post-processing of the raw high frequency (10 Hz) data to obtain fluxes representative of thirty minute periods involved the standard spike filtering, planar rotation of velocities, lag correction for CO₂ and water vapour concentrations, and calculation of mass fluxes using conventional equations (Moncrieff et al., 1997; Aubinet et al., 2000).

Carbon dioxide flux (F_{CO_2}) was also corrected to include the canopy storage flux using the simple approach of assuming that the CO₂ is uniformly distributed within the air column between the soil surface and the inlet of the tube:

$$F'_{\text{CO}_2} = F_{\text{CO}_2} + \Delta_{\text{CO}_2} \cdot \frac{h \cdot 1000}{\eta \cdot t} \quad (2)$$

where F'_{CO_2} is the corrected flux ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), F_{CO_2} is the flux measured by the eddy covariance system ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), Δ_{CO_2} is the difference in CO₂ concentration between t^0 and t^{-1} (ppm), h is the height of the air column (16 m), η is molar volume of an ideal gas (22.4 l mol⁻¹), the factor 1000 converts l into m³, and t is the time step of 1800 s.

After calculation of the fluxes the eddy-covariance data were combined with and fitted against microclimate data. Nighttime carbon dioxide flux (F_n), a surrogate for ecosystem respiration, was regressed against soil temperature at 7 cm depth (T_s) and soil moisture (RPAW, Eq. 1). Only data with a coincident friction velocity (u^*) greater than 0.25 m s⁻¹ were used for this analysis. Since details of the equations for modelling

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night time respiration were derived during the data analysis, the further treatment of the data is described in the “Results” chapter. The modelled ecosystem respiration was then used to calculate canopy assimilation (F_P) from the daytime fluxes:

$$F_P = F'_{CO_2} - F_R \quad (3)$$

- 5 Canopy assimilation was then fitted against global radiation measured above the canopy by means of a hyperbolic function (von Stamm, 1994):

$$F_P = F_{P,sat} \cdot \text{TANHYP}\left(\frac{k \cdot I}{F_{P,sat}}\right) \quad (4)$$

where k is an empirical coefficient describing the initial slope of the light response curve and I is the incoming short-wave radiation ($W m^{-2}$).

- 10 Canopy conductance, g_c , defined as the surface conductance to water vapour transfer at a canopy scale, was calculated from the eddy flux data as described by Jensen and Hummelshøj (1995) and Herbst et al. (2002). First, the total resistance, r_s , of the system was calculated as the quotient of vapour pressure deficit, VPD, of the air above the forest and water vapour flux, E . Analogously, the resistance owing to turbulent transport in the atmosphere, r_a , (assumed to be equal for momentum and water vapour) was determined as the quotient of mean horizontal windspeed, u , and the square of the friction velocity, u^{*2} . The resistance through the viscous sublayers on the individual leaves, r_b , was estimated as a function of the kinematic viscosity of the air, the molecular diffusivity of water vapour, the size of the leaves, the leaf area index, and the friction velocity (Jensen and Hummelshøj, 1995). Finally, canopy conductance was
20 calculated as the reciprocal of the residual resistance (Eq. 4):

$$g_c = \left(\frac{VPD}{E} - \frac{u}{u^{*2}} - r_b \right)^{-1} \quad (5)$$

- If VPD is given in $g m^{-3}$, E in $g m^{-2}$, u and u^* in $m s^{-1}$, and r_b in $s m^{-1}$, g_c is obtained in $m s^{-1}$. To convert g_c into the common plant physiological unit of $mmol m^{-2} s^{-1}$, a
25 multiplication factor has to be applied which is roughly 40 000.

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In order to obtain an indication of the sensitivity of the regulation of canopy conductance to ambient humidity, g_C was plotted against the actual water vapour pressure deficit of the air (VPD, mbar) for distinct periods of between two and four weeks with different levels of soil moisture. Each data set was fitted separately to the following equation:

$$g_C = \frac{g_{C,\max}}{c \cdot \text{VPD}^2} \quad (6)$$

where $g_{C,\max}$ is a theoretical maximum conductance that occurs when VPD (kPa) is zero (set constantly to $2000 \text{ mmol m}^{-2} \text{ s}^{-1}$ in that study), and c is an empirical coefficient that provides a measure of the sensitivity of the regulation of g_C . Envelope functions covering 90% of the data were fitted to the data by quantile regression (Cade and Noon, 2003). The seasonal course of the coefficient c in Equation 6 reveals how the canopy acclimates to changing conditions. This function is simpler and more empirical than the “Ball/Berry-Function” (Ball et al., 1987) that is commonly used but c is defining the shape of the response curve in the same way and reveals the same seasonal pattern as the coefficient D_0 in the Ball/Berry approach does. We chose the more empirical function because we did not want to derive physiological parameters top-down for a physiologically heterogeneous system like a savanna.

3 Results

3.1 Climate and phenology

Since 2002/2003 was a respectively dry year, periods with low rainfall during the wet season resulted in periods of low soil moisture even during the typical vegetation growth period (Fig. 2, Table 1). Therefore, the observational data during the growing season were divided in the following sub-sets (Table 1).

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3.2 Sectoral analysis and differences between savanna sites

For a sectoral analysis data were sorted according to wind direction in order to examine differences between the two savanna types. Data from the sector between 105° – 196° were taken for the fine-leaf *Acacia* savanna, from the sector between 270° – 76° for the broad-leaf *Combretum* savanna. Data from other wind directions were discarded. Figure 3a and b show light response curves of net ecosystem exchange of carbon dioxide (F_C) and of canopy photosynthesis (F_P) for the two sectors during the peak of the growing season (Period 3 as defined in Table 1). Since these curves show no significant differences between the savanna types in terms of fluxes, data were pooled again for further analysis. Consequently, the following paragraphs will show a principle analysis of carbon flux responses to water relations in a savanna ecosystem without considering possible small differences between the sub-types.

3.3 Night time respiration

In a first approach, the night time data sets identified for the analysis of the nocturnal fluxes after u^* filtering (1247 records) were divided into three classes of relative soil water content. Within each of these classes an exponential temperature response curves was generated. The analysis revealed a clear exponential increase of ecosystem respiration with increasing temperature and also a positive influence of soil moisture (Fig. 4). In addition, the data showed that the temperature response was modified by soil moisture: at low soil moisture the Q_{10} -value of the temperature function was reduced in comparison to high soil moisture. Unsurprisingly, we did not find seasonality in the temperature or moisture controls on respiration (not shown), since seasonal changes in flux rates due to changes in biomass and activity correlate with changes in temperature and rainfall patterns and are “masked” by the temperature and soil moisture response curves (Kutsch et al., 2001b). The relatively high Q_{10} -value for wet conditions (~ 2.5) indicates a hidden seasonal change in activity. This was confirmed by comparing mean night time fluxes throughout the year: highest respiration rates were

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found at the onset of the wet season in January and February, followed by constant decrease thereafter that was overlaid by a less severe influence of water shortage during the growing period (Fig. 8c). It is also noteworthy, that the temperature and moisture normalized value $R_{\text{eco,ref}}$ (in our study normalized to 15°) was higher during the dry season than during the wet season (Fig. 8c) which might indicate a higher substrate availability for heterotrophic soil respiration as also suggested by Augustine and McNaughton (2005).

The data set was fitted to the ecosystem respiration model described by Reichstein et al. (2002). This model provides response curves for soil moisture and temperature, and changes the Q_{10} -value of the temperature response curve with changing soil moisture as observed in this study:

$$R_{\text{eco}} = R_{\text{eco,ref}} \cdot f(T_{\text{soil}}, \text{RSWC}) \cdot g(\text{RSWC}) \quad (7)$$

$$f(T_{\text{soil}}, \text{RSWC}) = e^{E_0(\text{RSWC}) \cdot \left(\frac{1}{T_{\text{ref}} - T_0} - \frac{1}{T_{\text{soil}} - T_0} \right)} \quad (8)$$

$$g(\text{RSWC}) = \frac{\text{RSWC} - \text{RSWC}_0}{(\text{RSWC}_{1/2} - \text{RSWC}_0) + (\text{RSWC} - \text{RSWC}_0)} \quad (9)$$

where E_0 was not fixed but a linear function of relative water content (RSWC) allowing for a RSWC effect on temperature sensitivity. RSWC used as by Reichstein et al. (2002) was derived from the RPAW for the 0–10 cm layer by:

$$\text{RWSC} = \frac{\text{RPAW}}{100} \quad (10)$$

Figure 5 shows the modelled versus measured rates. Results indicate that this model approach explains much of the variation in flux rates and confirm the hypothesis about an indirect effect of water availability on ecosystem respiration via changes of temperature sensitivity (Q_{10}) for which Reichstein et al. (2002) developed their model expression. They discuss several mechanisms that may account for this variation. The first reason may be that labile substrates are concentrated in the upper soil which dries

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out earlier. Also differences between roots, rhizosphere and bulk soil in Q_{10} as well as water availability may occur (Boone et al., 1998). In particular for savanna ecosystems, another mechanism is important that was recently described by Tang et al. (2005) and Moyano et al. (2007). They showed that aboveground photosynthesis drives soil respiration with a time delay of 7–24 h. Higher availability of assimilates may also increase the Q_{10} value of the system.

3.4 Seasonal characteristics of canopy conductance and photosynthesis

VPD response curves of g_C plotted for each of the defined periods as envelope curves based on a 90% quantile regression (Fig. 6) showed that stomatal sensitivity changed drastically within a few days when soil moisture varied. The response curves are paired. Each pair shows data from a period with high soil water content (left) and data from a dryer period thereafter (right). In order to demonstrate the degree of stomatal acclimation the response curve from the left dataset is also shown in the right one (grey line). Stomatal responses to environmental conditions were highest in January (6a) and March (6c). The short period of drought during February (6b) slightly increased sensitivity to VPD, whereas during April (6d) the drought led to much-reduced canopy conductance over the whole range of VPD. After a large rainfall event in May (6e), plants reverted the regulation pattern again but did not reveal as high conductance as in January or March, indicating the onset of the senescence of the leaves that may be speeded up by the April drought period. Nevertheless, the following dry period during May (6f) reduced stomatal conductance again while the senescence of the plants went on. Consequently, a rainfall event during late June did not reverse the performance any more (6g) and the during the dry season (August), canopy conductance was reduced to a minimum (6h). The annual courses of the coefficient c in Equation (5), describing the sensitivity of canopy conductance to VPD is summarized in Fig. 9a.

Light saturated canopy photosynthesis was limited strongly by canopy conductance below a threshold of $250 \text{ mmol m}^{-2} \text{ s}^{-1}$ during all of the periods under consideration (Fig. 7a–h). During the periods with low soil moisture (right figures) canopy con-

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ductance did almost never exceeded this threshold and CO_2 uptake by the canopy was almost constantly reduced. In addition, the few data sets with a canopy conductance around $250 \text{ mmol m}^{-2} \text{ s}^{-1}$ suggest a decrease of the photosynthetic capacity, which means that photosynthetic capacity was strongly coupled to stomatal sensitivity. In addition, a seasonal trend of photosynthetic capacity with an increase towards March and a decrease thereafter can be seen (Fig. 9b).

Water use efficiency (WUE) revealed a slightly hyperbolic decrease with increasing VPD in each single period and was slightly higher during the wet season (Fig. 8a–h). This might reflect the lower activity of the canopy (the *Combretum* species dropped their leaves and the grasses desiccated in May) and the resulting higher proportion of evaporation during the dry season. Nevertheless, the water use efficiency seemed to be the most constant parameter during the whole season, again indicating a strong coupling between stomatal conductance and photosynthetic capacity.

The seasonal trends of all important parameters are summarized in Fig. 9a–c. The coefficient c (Eq. 5) is an indicator for the sensitivity of canopy conductance to VPD, $F_{P,\text{max}}$ for the photosynthetic capacity. R_{av} is the average nighttime respiration for each period and R_{15} the normalized respiration rate at 15°C and optimum water conditions. Each of these parameters showed a seasonal trend (dashed grey line) that was overlaid by mid-term responses to the respective drought periods, but the specific characteristics were different. The seasonal trend of $F_{P,\text{max}}$ was an increase until March and a decrease thereafter – a typical performance for a plant canopy during the course of the growing season. Night time respiration seemed to be highest at the onset of the growing season, was stable on a slightly lower level during the main part of the growing season and decreased thereafter. This trend was overlaid by depressions during the drought periods, in particular in April. The initially high respiration rate is typical for seasonal ecosystems facing drought or frost periods (Arneth et al., 2006; Schimel and Mikan, 2005).

The seasonal trend of the coefficient c revealed a broad minimum from January to March and constantly increased during the transition period towards the dry season.

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C also revealed mid-term responses to the drought periods. In order to distinguish between the seasonal trend and mid-term drought response c was plotted against the relative plant available water (RPAW) in Fig. 10. The seasonal trend is symbolized by the light grey arrow: three different levels of regulation – corresponding to main growing season, transition time and dry season – can be distinguished. Within each level the response to drought is symbolized by the dark arrows: during water stress (low RPAW) c is increased and shows the more conservative regulation of the stomata. Figure 11 summarizes the close relationship between stomatal regulation and photosynthetic capacity by the close relationship between canopy photosynthetic capacity and canopy conductance (Fig. 11a) and, in addition, a strong correlation between coefficient c and canopy photosynthetic capacity (Fig. 11b) for the 8 periods under consideration.

4 Discussion

The convergence of the two savanna types in terms of flux properties may be the most surprising result of this study. Sectoral analysis of flux data has been conducted successfully in other studies, where distinct differences in fluxes between sectors could be related to differences in properties such as species composition or LAI of the canopy (Kutsch et al., 2005). At this site the fluxes were identical in spite of different soil properties and plant species composition as described by Scholes et al. (2001). Since flux measurements by means of eddy-covariance cannot reveal eco-physiological details of adaptation at species level the reasons for the functional convergence of the savanna sub-types could only be found by detailed studies on leaf-level eco-physiology. Kutsch (unpublished data) could show a spatial correlation between soil properties and eco-physiological strategies of the grass species. Summarizing these findings it seems that different species optimize their fluxes by balancing stomatal conductance and photosynthetic capacity between water availability (lower in the *Acacia*-site soils) and nutrient availability (higher in the *Acacia*-site soils). The resulting convergence allows to treat the data as one dataset in the following principle analysis of water-carbon interactions

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of fluxes in an African savanna ecosystem.

Maximum canopy-scale carbon dioxide fluxes at light saturation ($F_{C,sat}$: $-17 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$) and canopy-scale photosynthetic capacity ($F_{P,max}$: $-22 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$) reported in this study are comparable with other eddy-covariance studies of African savanna ecosystems, particularly when bearing in mind that the 2002/2003 growing season at Skukuza was characterised by an extremely low precipitation. Scanlon and Albertson (2004) measured fluxes from four savanna ecosystems along a precipitation transect across the Kalahari sands. They report values of $F_{P,max}$ between -15 and $-20 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ for the “drier end” of the transect (mean annual rainfall 365 and 407 mm). A similar range is also reported in Williams and Albertson (2004) for a mixed *Acacia-Combretum* savanna in Botswana receiving a mean annual rainfall of 400 mm, and by Veenendaal et al. (2004) for a Mopani-woodland in Botswana with 464 mm mean annual precipitation.

Scanlon and Albertson (2004), who collected only short-term data of a few days during the 2000 wet season, interpreted differences in the light response curves of F_C and the VPD response curve of water use efficiency between the sites as a long-term adaptation of the different vegetation types to the mean precipitation at each location. In our study we found a highly dynamic ecosystem response to environmental factors that may also be part of this adaptation. Our approach of defining different periods according to rainfall characteristics and soil moisture provided valuable qualitative insights.

In particular, it showed that the response of canopy conductance to VPD followed the soil moisture conditions very dynamically and that conductance and photosynthetic capacity were strongly coupled. Three findings are noteworthy:

1. The short-term regulation of canopy conductance was modified by a general seasonal trend and some mid-term acclimation to soil water conditions. This can be seen in the variation of the coefficient c in Figs. 9–11.
2. The most constant parameter was water use efficiency (Fig. 8) that was influenced

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by VPD during the day but the VPD response curve of water usage did change only slightly during the course of the growing season and decreased by about 30% during the transition from wet to dry season.

3. The regulation of canopy conductance and photosynthetic capacity were closely related, suggesting a complex regulation pattern (Fig. 11).

At leaf level, general hypotheses regarding what controls stomatal behaviour suggest that soil water stress modifies the characteristics of stomatal behaviour (Cowan and Farquhar, 1977; Tenhunen et al., 1987). Lambers et al. (1998) hypothesised that under dry conditions the regulation of stomatal conductance and therefore net photosynthesis rate is more controlled by water relations (optimisation of the water use efficiency, WUE), whereas under wet conditions nutrients, particularly nitrogen, are the major controlling factor (optimisation of the photosynthetic nitrogen use efficiency, PNUE). The suggestion by Lambers et al. (1998) was recently supported by Midgley et al. (2004) for trees of African savannas. Also Kutsch et al. (2001a) showed by means of model calculations that stomatal acclimation allows the plant to optimize for high carbon gain during periods of sufficient water supply and to save water during drought.

It is important to note that decreases in stomatal conductance in many plants are inter-related with decreases in photosynthetic capacity (Hall and Schulze, 1980; Schulze and Hall, 1982). Whereas those authors assumed an un-coordinated response of stomatal conductance and photosynthetic capacity to soil water stress (Schulze and Hall, 1982), Flexas et al. (2006a; 2006b) showed recently on the molecular level that stomatal closure triggers down-regulation of Rubisco either directly through its effects on chloroplast CO₂ concentration or mediated by some common signalling (e.g. a response to abscisic acid). Data from this study were obtained by eddy covariance at the ecosystem scale and show the same pattern of inter-relation between stomatal conductance and photosynthetic capacity as leaf-level studies.

However, it is important to stress that theories developed for individual plants or leaves cannot be scaled simply to the vegetation level because different water use

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strategies and life cycles may compete for the available water and in this situation a conservative strategy may simply lead to a higher water usage by the competing neighbour (Schulze et al., 2005). Moreover, different plant functional types have different traits and life cycles that may influence the ecosystem properties much more than leaf scale acclimation. E.g. the reduction of water use efficiency at the end of the wet season might be due to the senescence of the grass biomass and a change from a dominance of the more water-efficient C_4 - to a dominance of C_3 -photosynthesis in the evergreen *Acacia* species. Further studies including detailed process analyses and multi-species canopy modelling are highly required to explain the adaptive inter-relation of canopy conductance and photosynthetic capacity which is only poorly represented in higher-scale models.

Respiratory patterns showed a strong dependency on temperature and soil moisture. In addition higher rates during the early stages of the wet season and a decrease thereafter even in periods of high soil moisture was detected. It is assumed that this is due to the growth respiration of the new biomass and the mineralization of easily decomposable organic matter that has been accumulated during the dry season. Augustine and McNaughton (2005) showed recently that the new growing plant biomass at the onset of the growing season is also favoured by a large inorganic nitrogen pool that has accumulated during the dry season, during which mineralization does not completely cease. Xu et al. (2004) found a similar pattern oak/grass savanna ecosystem in California. They also observed a 'respiratory flush' after a rainfall event, as did Levine et al. (1996) at Pretoriuskop (30 km south of the Skukuza site) and Scholes et al. (1997) in savannas at Nylsvley, South Africa.

5 Conclusions

The eddy covariance measurements at a flux tower close to Skukuza in the Kruger National Park, South Africa, revealed the strong influence of water relations on the carbon fluxes in savanna ecosystems. It also gave useful insights into the acclimation

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of the plant canopy to changing conditions.

Drought affected the carbon fluxes in the savanna ecosystem under consideration at several processes. From the eddy covariance data alone it is unclear whether interactions of these processes exist. E.g. a reduction of photosynthesis during dryer period could affect the substrate availability of roots and mycorrhizae and consequently reduce the autotrophic soil respiration (Moyano et al., 2007; Tang et al., 2005). Therefore, further research, e.g. on the partitioning of soil respiration under changing soil moisture are highly recommended for further research.

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Table 1. Sub-sets for data evaluation in 2003.

Dataset No.	Period	Characterization	Mean RPAW 0–10 ^a
1	25 January–8 February	Wet soil, early wet season	30.6
2	10–20 February	Dry soil, early wet season	16.1
3	23 February–29 March	Wet soil, mid wet season	28.2
4	1–25 April	Dry soil, mid wet season	11.6
5	27 April–11 May	Wet soil, transition period	39.1
6	14 May–6 June	Dry soil, transition period	12.7
7	14 June–12 July	Wet soil, dry season	28.2
8	28 July–3 September	Dry soil, dry season	9.7

^a Averages were build on the basis of only those datasets that contained full information (climate and EC) after quality control and filtering. They might slightly differ from the “real” averages.

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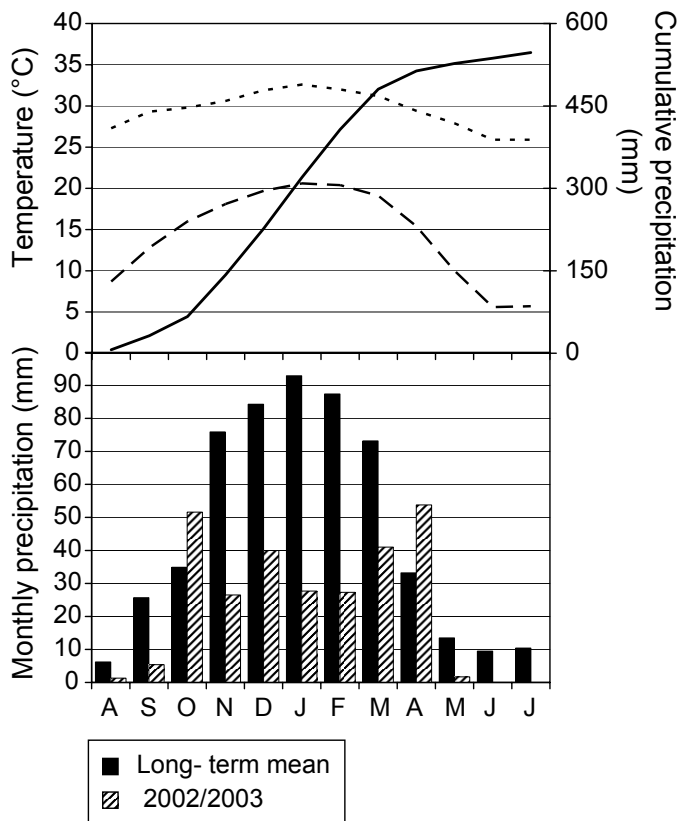



Fig. 1. Long-term monthly means of minimum and maximum temperature (dotted lines) and the mean precipitation (solid line) at Skukuza (data from 1960–1999, after Scholes et al., 2001). Precipitation is shown as cumulative curve. In order to show a complete growing season the data are printed from August to July. In the lower part the monthly precipitation of the growing season 2002/2003 (hatched bars) is compared to the long-term mean (black bars).

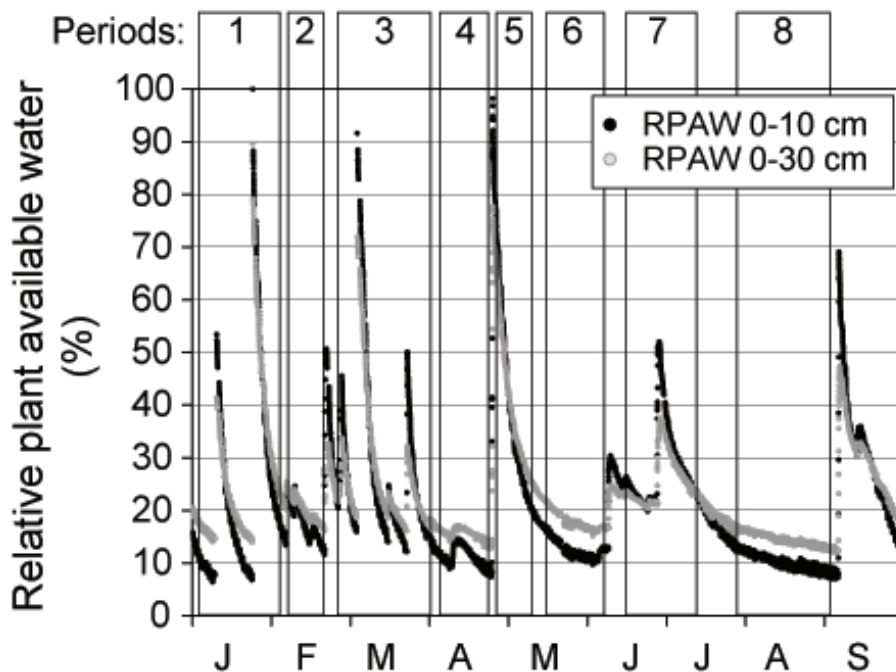


Fig. 2. Seasonal course of relative plant available water (RPAW) for the layers 0–10 cm and 0–30 cm. The periods defined in Table 1 are marked in the Figure.

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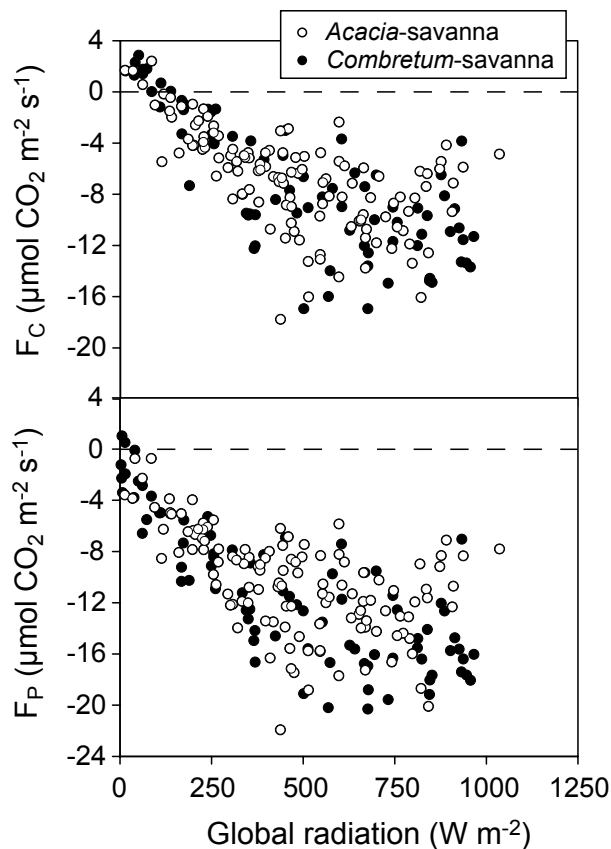


Fig. 3. Light response curves of net ecosystem exchange (F_C , upper graph) and canopy photosynthesis (F_P , lower graph) measured during the peak of the growing season (Period 3 in March 2003). The open symbols show data from the *Acacia*-site, the filled symbols from the *Combretum*-site.

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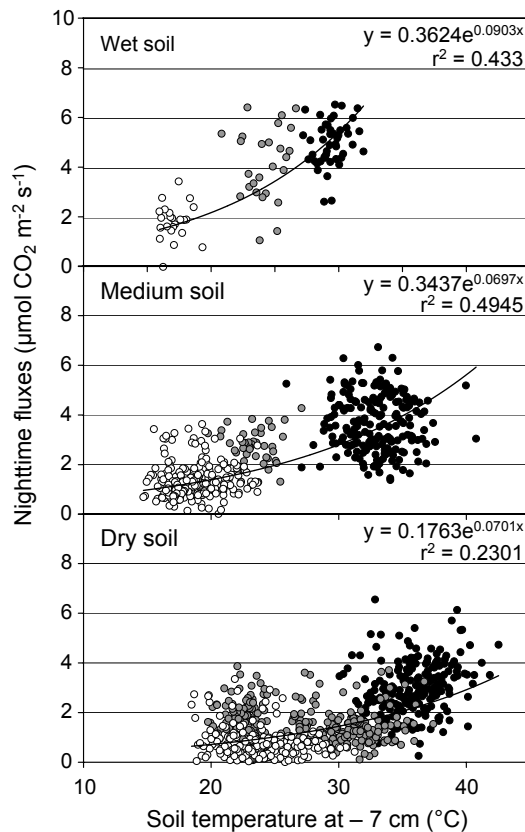


Fig. 4. Temperature response curves of nighttime respiration for different intervals of soil moisture. Filled circles symbolize data from the main growing season (January–March 2003), grey circles from the transition time (April–May 2003) and open symbols from the dry period (June–September 2003). The values of the exponential fits and the regression coefficient are related to the whole datasets comprising data from all seasons.

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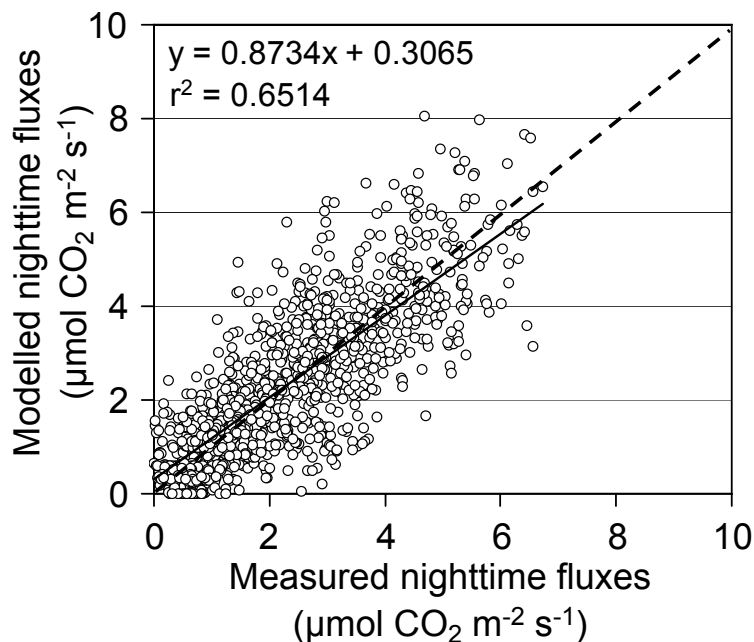


Fig. 5. Comparison between measured and modelled data of nighttime respiration. Based on complete data set (January–September 2003). The solid line represents the regression (regression values written at the top), the 1:1 line is dashed.

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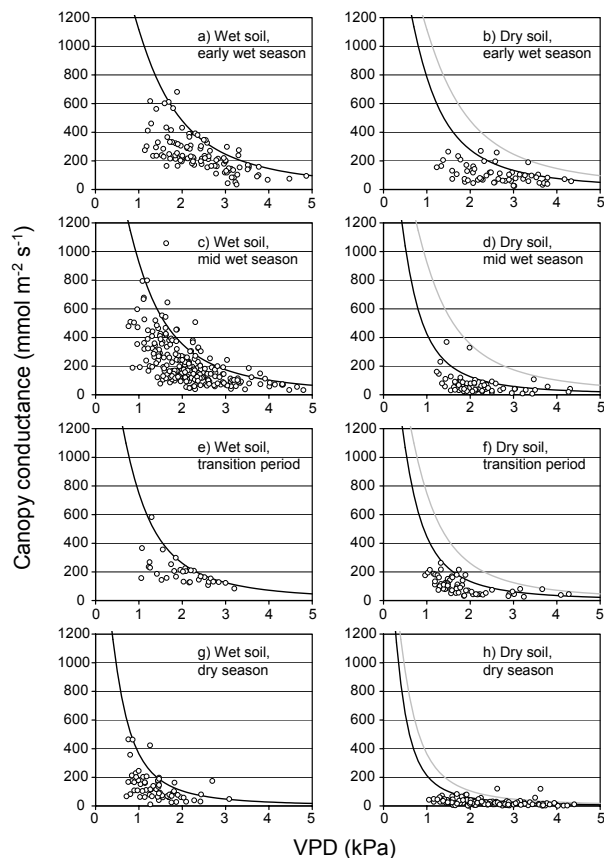


Fig. 6. VPD-response curves of stomatal conductance for the 8 periods as defined in Table 1. Data measured at saturating light conditions with incoming shortwave radiation being higher than 700 W m^{-2} . The grey curves in the situations with dry soil (right graphs) symbolize the curves from corresponding situations with wet soils (left graphs).

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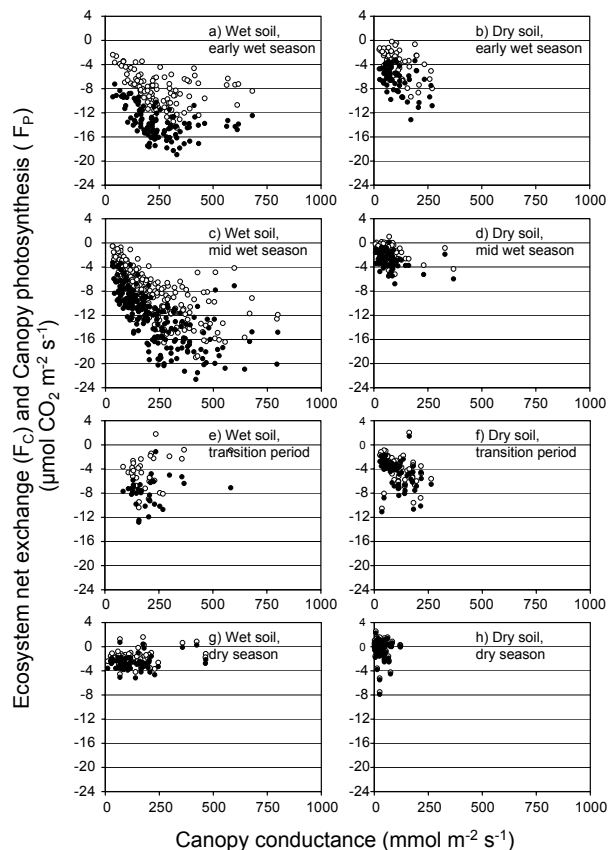


Fig. 7. Conductance response curve of CO_2 -fluxes for the 8 periods as defined in Table 1. Black dots symbolize the canopy gross photosynthetic flux, open circles the net ecosystem flux; data measured at saturating light conditions with incoming shortwave radiation being higher than 700 W m^{-2} .

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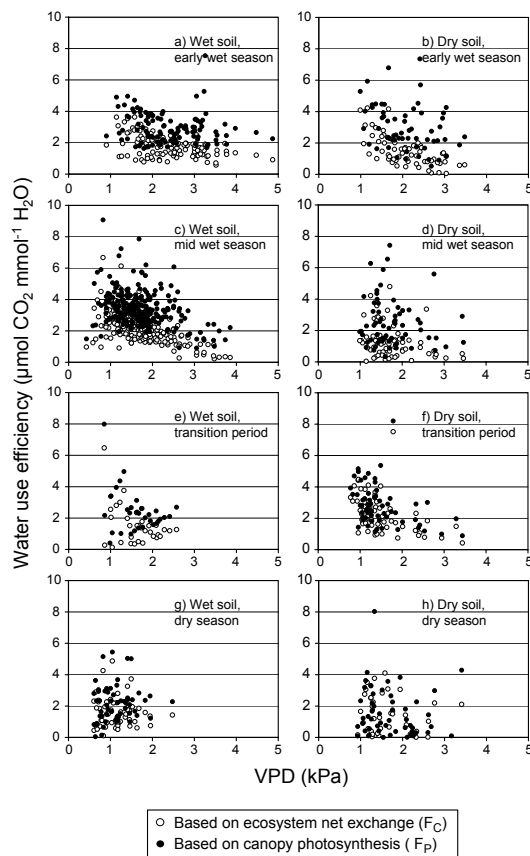


Fig. 8. Response curve of water use efficiency (WUE) to VPD for the 8 periods as defined in Table 1. Black dots symbolize the WUE based on canopy gross photosynthetic flux, open circles the WUE based on net ecosystem flux; data measured at saturating light conditions with incoming shortwave radiation being higher than 700 W m^{-2} .

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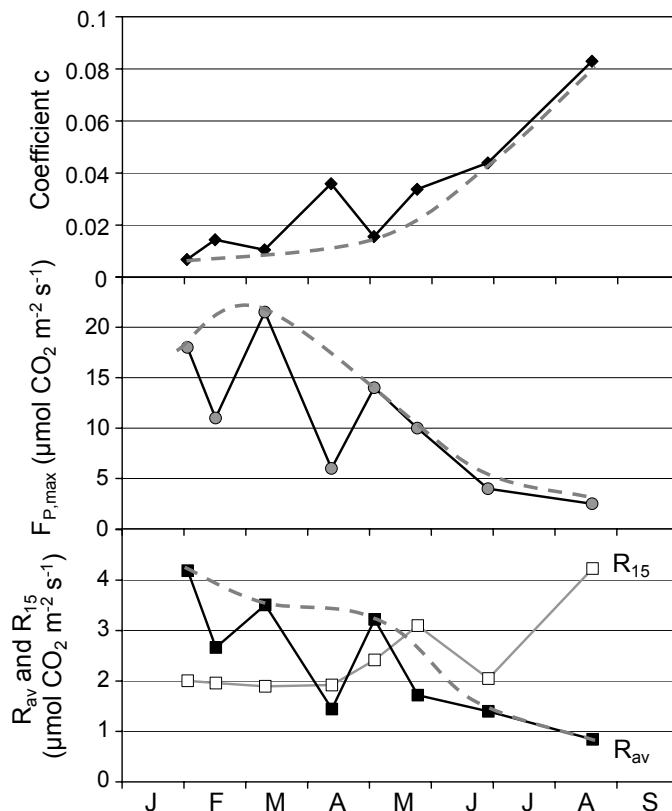


Fig. 9. Annual courses of the coefficient c describing stomatal response sensitivity to VPD, of maximum canopy photosynthesis ($F_{p,max}$) average nighttime respiration (R_{av}) and R_{15} as derived from the model. Each point represents the center of a period defined in Table 1. The dashed line shows a hypothetical seasonal course without intermediate drought periods.

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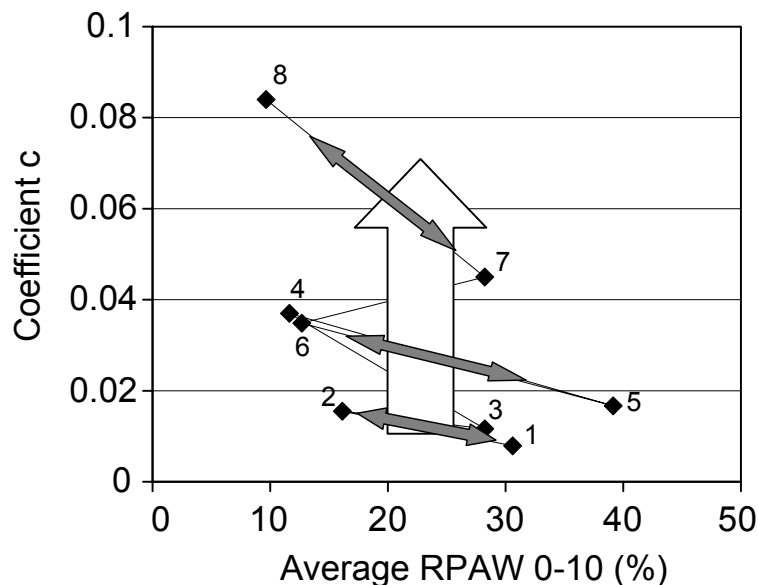


Fig. 10. Relationship between the coefficient c describing stomatal response sensitivity to VPD and soil moisture during different periods of the growing season as defined in Table 1 and symbolized by the numbers beside the data points. Three different periods of regulation – corresponding to main growing season (1–3), transition time (4–6) and dry season (7–8) – can be distinguished. The general trend throughout the growing season is symbolized by the big, light grey arrow. Within each period the response to drought is symbolized by the dark arrows: during water stress (low RPAW) c is increased and shows the more conservative regulation of the stomata.

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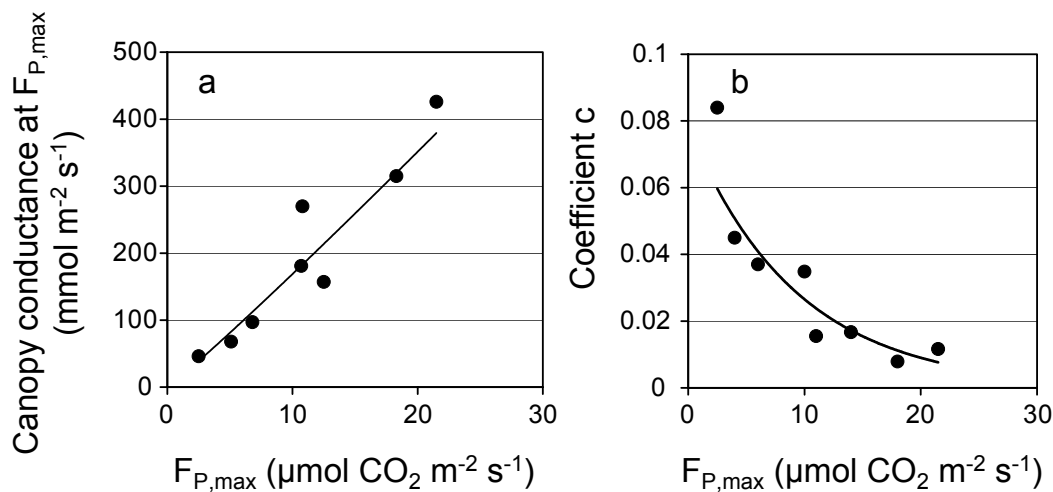


Fig. 11. Relations between photosynthetic capacity ($F_{P,max}$) and canopy conductance at $F_{P,max}$ (a) and between $F_{P,max}$ and the coefficient c describing stomatal response sensitivity to VPD (b) for the 8 periods under consideration.

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